Meerkat close calls encode group-specific signatures, but receivers fail to discriminate

Townsend, S W ; Hollén, L I ; Manser, M B

Abstract: A great deal of variation is known to underlie the vocalisations of animals. Calls can for example vary among individuals or between social and behavioural contexts. Calls also have the potential to vary between groups. Many group living animals are known to produce stereotyped group-specific calls and such group signatures are thought to play a role in territory defence or indeed mate choice. Group signatures are generally found in long-distance call variants that work to maintain contact between group members, sometimes referred to as "contact calls". Cooperatively breeding, territorial meerkats (Suricata suricatta) also use contact calls, potentially to maintain social organization during foraging. However, these contact calls are generally quieter, than long distance calls in other species, and better described as "close calls". We investigated whether these similar call types also possess group-specific signatures and whether any such variation is used by receivers. We recorded close calls from 71 individuals belonging to 10 different meerkat groups. We found that such close calls do indeed possess group signatures, but that this underlying variation does not appear to be used by receivers, possibly because meerkats use other sensory systems to identify non-group members. We stress the importance of conducting playback experiments when investigating group-specific vocal signatures and use our results as a basis for predicting which animals may rely on group information encoded within close calls.

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Meerkat close calls encode group-specific signatures, but receivers fail to discriminate.

Simon W. Townsend [1,2], Linda I. Hollén[1,2], Marta B. Manser[1,2]

1 Animal behaviour group, Institute of Evolutionary Biology and Environmental Studies, Universität Zürich, Switzerland

2 Kalahari Meerkat Project, Kuruman River Reserve, South Africa

Correspondence to: Simon W. Townsend, Verhaltensbiologie, Institute of Evolutionary Biology and Environmental Studies, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland, Tel. ++41/(0)44/6355277, Fax +41/(0)44/6355490, email simon.townsend@ieu.uzh.ch

Postal address: Marta B. Manser, Verhaltensbiologie, Institute of Evolutionary Biology and Environmental Studies, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

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ABSTRACT

A great deal of variation is known to underlie the vocalisations of animals. Calls can for example vary among individuals or between social and behavioural contexts. Calls also have the potential to vary between groups. Many group living animals are known to produce stereotyped group-specific calls and such group signatures are thought to play a role in territory defence or indeed mate choice. Group signatures are generally found in long-distance call variants that work to maintain contact between group members, sometimes referred to as "contact calls". Cooperatively breeding, territorial meerkats (Suricata suricatta) also use contact calls, potentially to maintain social organization during foraging. However, these contact calls are generally quieter, than long distance calls in other species, and better described as "close calls". We investigated whether these similar call types also possess group-specific signatures and whether any such variation is used by receivers. We recorded close calls from 71 individuals belonging to 10 different meerkat groups. We found that such close calls do indeed possess group signatures, but that this underlying variation does not appear to be used by receivers, possibly because meerkats use other sensory systems to identify non-group members. We stress the importance of conducting playback experiments when investigating group-specific vocal signatures and use our results as a basis for predicting which animals may rely on group information encoded within close calls.

KEYWORDS: Contact calls, group signatures, meerkats, playbacks, vocalisations

45 INTRODUCTION

46

47 From over five decades of research a clear picture has emerged which suggests substantial
48 variation underlies the vocalizations of non-human animals (Hauser 1996). Whilst variation can
49 occur at a number of discrete levels, much work has focused on acoustic differences between
50 distinct behavioural contexts, primarily because of the cognitive implications associated with
51 such potential semantic communication (Cheney & Seyfarth 1990, 2007). This concentration has
52 ultimately led to a slight neglect for other relevant causes of variation, their perception and the
53 appropriate response, that may in fact require no less sophisticated cognitive processing (Tibbetts
54 & Dale 2007). Calls can, for example, vary considerably at the individual level, a phenomenon
55 documented in numerous species across the animal kingdom (e.g. Birds; Sharpe & Hatchwell
56 2005, Mammals: Rendall et al. 1996; McComb et al. 2000, Amphibians: Ryan et al. 1996), but
57 also variability can result from differential group membership. This may be particularly true for
58 common calls used to maintain group cohesion (Vehrencamp et al. 2003), and help in allowing
59 individuals to distinguish between group and non-group members.

60

61 Primates and some cetaceans are known to exhibit group specific acoustic differences and
62 discriminate between familiar and unfamiliar individuals (Primates: Mitani et al. 1992; Mitani &
63 Gros-Louis 1998; Crockford et al. 2004; Herbinger et al. 2009; Cheney & Seyfarth 1990, 2007;
64 Rendall et al. 1996, Cetaceans: Ford 1991; Tyack 2000). A number of species of primates and
65 cetaceans live in complex, fission-fusion social groups, and in some cases defend their territories
66 aggressively (Wilson et al. 2001). Hence the selective advantages driving the evolution of group
67 signature calls are likely to include maintenance of social bonds (Tyack & Sayigh 1997;

68 Crockford et al. 2004), negotiation of group decisions (Balsby & Scarl 2008; Scarl & Bradbury
69 2009) and possibly territory marking (Brown & Farabaugh 1997; Wright & Wilkinson 2001;
70 Crockford et al. 2004).
71
72 Group living birds also provide examples of vocal group signatures. The contact calls of parrots
73 and budgerigars (Melopsittacus undulatus) have been shown to vary at the group level and
74 consequently, this commonly produced social vocalization has been suggested to facilitate group
75 identification (Bradbury 2003; Hile & Striedter 2000; Vehrencamp et al. 2003). From a
76 functional perspective, group signatures in birds may play some role in mating strategies. For
77 example, song sparrows (Melospiza melodia) discriminate more (in terms of attempted
78 copulations) to the songs recorded from distant groups than nearby groups (Searcy et al. 2002); a
79 behaviour previously explained through invoking the local adaptation hypothesis. This theory
80 suggests females benefit from mating with local males because such males have genes adapted to
81 local conditions (Baker & Cunningham 1985; Searcy et al. 2002). As such discrimination can
82 have a considerable effect on fitness (less adapted offspring), it represents a very plausible
83 selective pressure acting on the evolution of group signatures in birds.
84
85 One cross-species commonality that exists for group specific signatures is their occurrence in the
86 long distance calls of animals. Chimpanzees (Pan troglodytes verus) for example exhibit group
87 differences in their pant-hoot vocalizations which can travel over 1 km through dense forest
88 environments and as previously noted these signatures probably play a role in signaling territory
89 boundaries to neighbouring communities (Wilson et al. 2001). The contact calls of parrots
90 (Vehrencamp et al. 2003) and the “screech” contact calls of greater spear-nosed bats

(Phyllostomus hastatus)(Boughman 1997) also appear to show group specificity, keeping contact between individuals over long distances.

But what about species that also use calls for group coordination and exhibit territorial behaviour towards extra-group members, yet exist together in cohesive foraging parties? Do these calls, typically given to close-by group members, also exhibit group signatures and what adaptive function would it have in this social setting? To address these questions on group signatures and their adaptive function, we investigated both the variation that underlies meerkat (Suricata suricatta) close calls and whether any information in these calls is used by receivers. Close calls are the most commonly emitted meerkat call type, being produced during social foraging contexts every 5 to 20 seconds. Acoustically, close calls can be described as short, pulsated, medium frequency (600-1000Hz) calls which can travel up to 20m (see Fig 1) and similarly to contact calls in other animal species (Vehrencamp et al. 2003), likely play an important role in the maintenance of group-cohesion and spacing between group members (Manser 1998). To date, many studies investigating group-specific signatures have either focused on their production (Mitani et al. 1992; Smolker & Pepper 1999; Crockford et al. 2004; Nousek et al. 2006) or their discrimination by receivers (McComb 2000; Searcy et al. 2002; Vehrencamp et al. 2003) and have not necessarily integrated both signaling aspects together. This is a crucial perspective to take if we are to understand the adaptive function and relevance of such variation.

Meerkats are diurnal, cooperatively-breeding, desert-adapted mongooses that live in social groups of between 3-50 individuals (Clutton-Brock et al. 2008). Breeding is generally restricted to the dominant pair (Griffin et al. 2004) and all other subordinates help in rearing the offspring

through partaking in various cooperative behaviours (Clutton-Brock et al. 2001). They possess a correspondingly complex vocal system with an integrated urgency-based and functionally referential alarm call system (Manser 2001), and other context specific call types used to coordinate group behaviour (e.g. sentinel calls, lead calls, moving calls, Manser 1998; Bousquet, pers. comm.). Meerkats spend the majority of their time socially foraging in groups on the ground digging for invertebrate prey (Doolan & McDonald 1996), where their vision is somewhat obstructed. Furthermore at different times of the year, their natural habitat can become densely vegetated, again restricting the vision medium even more. Vocalisations therefore play a crucial role in keeping individuals continually informed of changes in the social and ecological environment. Meerkats are also highly territorial, occupying defined home-ranges and defending their territory boundaries aggressively against foreign individuals, such as roving or intruding males (Young & Monford 2009). When spotting a foreign meerkat, an individual typically interrupts foraging and focuses on them, alerting the rest of the group to it. Often the group then adopts a stereotyped "raised tail" posture and moves rapidly towards the group, otherwise known as the "war dance".

Given the territorial nature of meerkats, being able to continually recognise they are surrounded by conspecific group members could be advantageous, reducing additional territorial defense costs against intruders, roving groups of males, or evicted females, looking for reproductive opportunities. Combining this with the critical role played by the vocal medium in meerkat daily lives, we investigated whether meerkats might exhibit group specific close calls, and if receivers can differentiate between close calls produced by members from other groups in comparison to their own. In addition, because it has been indicated that discrimination between own and

foreign-group calls can be influenced by the relationship residents have with surrounding groups, the so called "dear enemy" or "nasty neighbour" effect (Wilson 1975; Muller & Manser 2007**;** Akcay et al. 2009), we further differentiated "foreign group" close calls into neighbouring and stranger groups.

METHODS

Study population

Sound recordings and playback experiments were carried out on two populations of free living meerkats; at the Kuruman River Reserve (KRR population), which lies 30 km east of Van Zylsrus (Clutton-Brock et al. 1998), and in the Kalahari Gemsbok National park (park population) along the dry Nossob riverbed. As part of the Kalahari Meerkat Project`s long-term data collection, all animals in both populations were tagged with sub-cutaneous transponders (Clutton-Brock et al. 2001) and with haircuts or dye markings for individual identification. All subjects were habituated to a level that allowed recordings and observations within 0.5 m.

Individual and group differences

Because individual variation may explain some of the underlying variation between groups, we investigated first whether meerkats have individually distinctive calls and then whether when controlling for this variation, group differences persist with a high fidelity. We used calls from

between 4-10 individuals from 10 meerkat groups all belonging to the KRR population. All individuals included in the analyses were adults over 1 year of age of mixed sexes and status. The number of calls included for each individual varied between 6 and 10 (most groups had 10 different calls per individual) totaling 688 calls (range 36 – 98 per group). All calls were recorded between 2003-2006, apart from one group, Avatar, which was recorded in 1996. To exclude any possible differences in recording conditions between the two recording periods (1996 and 2003-2006) the test on group differences was repeated without Avatar and the results stayed the same.

Recording methods

We recorded close calls used in the acoustic analyses and for playback experiments at a distance of 1 to 2 m from the caller with a directional Sennheiser microphone (ME66 with K6 power module and a MZW66 pro windscreen, frequency response 40-20'000 Hz+- 2.5 dB, Old Lyme, Connecticut, U.S.A.) connected to a Sony digital audio tape recorder DAT-TCD D100 (frequency response: 20-20'000 Hz +-1 dB, 16 bit, 44.1 kHz) or a Marantz PMD-670. We uploaded the calls on to a PC notebook and digitized them with a 24-bit U24 waveterminal USB audio interface (Ego-sys, Seoul, Korea). Single calls with high signal-to-noise ratio were selected randomly for the acoustic analyses.

Fig 1

Acoustic analysis

We first conducted a 1,024-point fast Fourier transformation (Hamming window; time step: 1.45 ms; overlap: 98.43%; frequency range: 11.025 kHz; frequency resolution: 28 Hz) of all calls using Avisoft-SASLab pro 4.38 (R. Specht, Berlin). We measured four acoustic parameters manually in Avisoft: call duration, number of pulses, pulse duration and interval duration (see table 1). Six other parameters were measured with LMA 2005 (developed by K. Hammerschmidt), a software tool that extracts a variety of call parameters from acoustic signals (for detailed description of the algorithms and calculation of parameters, see Schrader & Hammerschmidt 1997). First, we calculated the median frequency of the first dominant frequency band. In tonal calls, this band represents the fundamental frequency, whereas in atonal signals like the close calls, the first dominant frequency peak reflects the frequency with the highest energy. Second, we determined the statistical distribution of spectral energy measured as the first and second quartiles of the distribution of frequency amplitudes in the spectrum. Third, we calculated the median peak frequency (the frequency with the highest amplitude in a time segment) and its location. Fourth, we determined the percentage of noise in each call.

Table 1

Playback experiments

We tested responses to close calls of their own group members versus close calls of neighbouring and foreign groups in 12 groups, 3 from the park population and 9 from the KRR population. For 6 of the groups, the foreign playback was from neighbour groups and for the other remaining 6

206 the playback was from distant stranger groups. Playback sound files were edited using Cool Edit
207 2000 (Syntrillium Software Corporation, Phoenix, Arizona, U.S.A.). Sound files included
208 uncompressed, high signal-to-noise ratio close calls of four different natal individuals, always
209 consisting of at least 1 adult male and female. The rate and amplitude (48 to 52 dB, measured at
210 0.3 m in front of the speaker (Voltcraft 329 Sound Level Meter, Conrad Electronic, Hirschau,
211 Germany; accuracy +-2 dB at 94 dB)) of the calls was kept as naturally observed in the different
212 groups simulating a group of four individuals foraging close by. While the subject group was
213 foraging, the loudspeaker (Sony SRS-A60, frequency response 70-20'000 Hz) was placed at a
214 distance of > 20 m in front of the group. Calls were then played from a Sony DAT-TCD D100
215 recorder, as soon as the first individual entered the 20 m distance range. Response variables
216 measured included the closest approach to the loud speaker during the 2-min playback (falling in
217 either of these categories: <1 m, 1-2 m, 2-5 m, 5-10 m) and the time that the individual who
218 approached closest (in case of more than one, the first individual to do so) spent within 5 m of the
219 loudspeaker during the time of the playback.
220
221 *Statistical analysis*
222
223 We conducted all analyses in SPSS (V.16.0) and R, version 2.8.1 (R Development Core Team
224 2008), using the software package "MASS" (Venables & Ripley 2002). To avoid correlated
225 predictor variables, we used spearman rank correlations to exclude acoustic parameters that
226 showed ≥ 85% inter-correlation. We then entered the remaining parameters into a Discriminant
227 Function Analysis (DFA) to determine the classification probabilities of close calls to individuals
228 within each group and to groups within the KRR population. Discriminant function analysis

identifies linear combinations of predictor variables that best characterize the differences among groups and combines the variables into one or more discriminant functions, depending on the number of groups to be classified. This analysis method provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). For external validation, we used a leave-one-out cross-validation procedure and to estimate the significance of the classification with direct DFAs, two-tailed binomial tests were used with a corrected level of chance corresponding to the number of categories discriminated between (Mundry & Sommer 2007). Since the data for group signatures were two factorial (group; individual) and contained more than 1 call exemplar per individual, it has been argued that conventional DFA provides grossly-inflated levels of overall significance of discriminability (Mundry & Sommer 2007). To control for this statistical conflict of "individual" and estimate the significance of the number of correctly cross-validated calls, we subsequently used a nested (individual within group) permutated DFA (pDFA) (Mundry, pers.comm.). Furthermore, to ensure no differences resulted from variation in dominance status and sex, we also performed a pDFA whilst keeping these two additional variables constant.

For the playback experiments, we analysed whether the closest approach to the loudspeaker (<1 m, 1-2 m, 2-5 m, 5-10 m) differed between playbacks of own versus foreign and neighbour versus stranger close calls using ordinal logistic regressions (for ordered dependent variables with > 2 categories). The time that the individual who approached the closest spent within 5 m of the loudspeaker during the duration of the playbacks was analysed with a paired (own - foreign) and unpaired (neighbour - stranger) t-test.

RESULTS

Individual differences within groups

For all 10 study groups, close calls could statistically be distinguished on the basis of individual identity (See table 2). Classification probabilities varied between 58 – 80 % with a mean of 59 ± 7 % (± SD) across the 10 groups and two tailed binomial tests showed that all classification probabilities were much higher than that expected by chance (16 ± 6%).

Table 2

Differences between study groups

When statistically controlling for individual we found that meerkat close calls possess group-specific acoustic signatures. A nested pDFA with 1000 permutations showed that close calls could correctly be classified on the basis of group (originally included elements 176/1000 permutations, P = 0.001; cross classified elements = 99.6/1000, P=0.001). With a more detailed analysis we also controlled for dominance status and sex, however, in this smaller subset of data, group still had a significant effect on the acoustic structure of close calls (originally included elements 70/1000 permutations, P = 0.040; cross classified elements = 61.8/1000, P=0.017)

Playback experiments

The probability of the closest approach being within 1, 2, 5 and 10 m of the loudspeaker during the 2-min playback did not differ between close calls of own and foreign group members ($Z = -0.16$, $P = 0.88$, Fig. 2), nor did it differ between playbacks of neighbour versus stranger close calls ($Z = -0.18$, $P = 0.86$, Fig. 2). Similarly, the time that the individual who approached closest spent within 5 m of the loudspeaker did not differ between the different treatments (own – foreign: $t = 0.53$, $N_1 = N_2 = 12$, $P = 0.61$; neighbour – stranger: $t = -0.22$, $N_1 = N_2 = 6$, $P = 0.83$, Fig. 3).

Figure 2 and 3

DISCUSSION

Our results show that meerkat close calls were individually distinctive, but more interestingly, when controlling for this variation, also encoded information regarding group identity. Subsequent playback experiments indicated that, whilst group differences existed, receivers appeared not to discriminate between them. These data therefore confirm numerous previous studies that have shown that geographic and individual variation underlies the social vocalizations of animals (Hile & Striedter 2000; Vehrencamp et al. 2003; Mitani & Gros-Louis 1998; Crockford et al. 2004), but contrasts others which suggest that group-specific vocal signatures are meaningful to recipients and have an important adaptive function in certain species (McComb et al. 2003; Vehrencamp et al. 2003; Herbinger et al. 2009). These findings are however in line with a recent study that reports significant individual variation in meerkat alarm calls, but no use of such variation (Schibler & Manser 2007).

297 In fluid social-living territorial animals that rely heavily on vocalizations as the primary
298 communicative medium, group-specific differences in call structure may play a vital role in
299 discrimination between residents and strangers (Crockford et al. 2004) and many playback
300 experiments in mammals and birds have shown that such group signatures are meaningful to
301 listeners (Herbinger et al. 2009). Whilst meerkats do not fission into sub-groups and generally
302 forage together as a cohesive social unit, they do exhibit territorial behaviour to stranger groups.
303 Furthermore, due to their foraging technique and the varying vegetation density throughout the
304 year, meerkats also depend heavily on vocalizations for group coordination and for information
305 on changes in the social and ecological environment. It is therefore plausible that at some level,
306 close calls may be important for allowing individuals to confirm they are surrounded by their
307 own and not extra-group members, reducing the costs associated with territorial guard. Our
308 playback experiments however showed no such discrimination, even when we differentiated at
309 the level of neighbour and stranger.
310
311 These findings have two important implications; firstly, just because acoustic differences exist, it
312 does not mean that they are salient to receivers. Such findings, also documented for individuality
313 in meerkat alarm calls (Schibler & Manser 2007), stress the importance of conducting playback
314 experiments to systematically confirm the perception of acoustic variability. Otherwise, without
315 this discrimination, it becomes difficult to make assumptions regarding the adaptive significance
316 of acoustic signatures.
317
318 Secondly, these results suggest that, at least in meerkat close calls, group signature has no
319 adaptive function: selection has not favoured a decoding of this information by receivers.

However, given the relatively small sample size (Neighbour-Stranger N=6) and the negative result obtained, it is important to briefly address alternative explanations for these findings. For example, it is possible that in fact meerkats did discriminate between own and foreign calls, at a very subtle level, in some behavioural parameter we did not measure. Whilst this is plausible, from observing natural inter-group encounters (pers. obsv), we feel that the response measures we choose sufficiently quantify meerkat interest in the acoustic stimuli we played back. Furthermore, it could be argued that such "irrelevance" may arise because the group signature signal is not reliable enough for selection to drive a use of this information in receivers. But, even when we controlled for multiple confounding factors, we still found a significant group signature presence in our discrimination analyses. We therefore alternatively propose that this irrelevance is more likely to arise from competing sensory modalities.

Whilst vocal communication is extremely important in meerkat daily lives (Manser 1998), they also have a well developed visual detection system, with designated guards undertaking sentinel duty (Clutton-Brock et al. 1999), searching for potential predators and, as a consequence of this, identifying foreign individuals. Olfactory cues are also crucial for predator or for foreign-group member detection, with individuals responding strongly to secondary predator cues (Manser et al. 2001) and the faeces of roving males (Mares, pers. comm). With this in mind it is plausible that, despite their pervasiveness, there has been less selective pressure for meerkats to perceive group-specific signatures in their close calls in comparison to other species where, due to their social system or their surrounding environment, vocal communication dominates over visual and olfactory mediums. If this really is the case, it could be predicted that animals exhibiting similar social organisation and close call types, but with limited visual contact, should possess group

specific signatures in their close calls, and also rely on this acoustic labeling for foreign individual identification. Baboons, especially those inhabiting forest environments (Ey et al. 2009), may provide a good, testable example. In such dense environments vision is restricted, to sometimes within 5m, enhancing the importance of the vocal communicative medium. Baboons are well known to use close "grunts" (Rendall et al. 1999) to coordinate group behaviour and maintain contact with each other, furthermore they show huge range overlap with other nearby groups and coming into contact with such groups can end in aggression and subsequent displacement. It is therefore possible that there has been more selective pressure for baboons to use contact calls, at least in this instance, as a means of extra-group member discrimination. Such a hypothesis stresses the importance of conducting playback experiments to test acoustic variability and could potentially be generalized across different call types and animal species.

Lastly, if such information on group membership is not used by meerkat receivers, at least in this particular context, then why have group signatures at all in close calls? In meerkat groups, breeding is generally restricted to the dominant pair, ultimately resulting in a high level of genetic relatedness (Griffin 1999) and hence physical similarities between individuals. If vocal characteristics are determined by physical characteristics (such as vocal tract morphology), as has been previously suggested (see Lieberman 1984), individuals that belong to the same group and are physically similar, will also produce acoustically similar calls (Crockford et al. 2004). Furthermore, given that vocal learning appears to be quite a common mechanism underlying variation in animal calling behaviour (Janik & Slater 1997), there could also be a social learning dimension to explaining why meerkats from the same group produce acoustically similar calls. This being said, genetic determination of vocal traits is probably a more parsimonious

366 explanation (Ryan et al. 1996) and given the consistent relatedness within meerkat groups, also
367 more plausible. However, before we fully rule-out the lack of adaptive function and the
368 irrelevance of such information, additional experimental paradigms with close calls, in different
369 social settings (for example, during roving, or eviction contexts), need to be undertaken.
370
371 Taken together our results suggest that considerable variation underlies the close calls of
372 meerkats. When controlling for individual variation, similarly to long-distance contact calls,
373 there were systematic differences between groups. But when experimentally testing whether
374 group differences are perceived, we found that meerkats do not appear to use this encoded
375 information, probably because their visual and olfactory systems play a more important role for
376 the recognition of foreign individuals. We think that these results further our insight into the
377 adaptive significance, or lack thereof, of group specific signatures in animals and encourage
378 future studies to take into account the contribution that different factors play in the underlying
379 variation of such calls.
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561 Table 1. Acoustic parameters included (measured by LMA and in Avisoft).

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563

563 Table 2. The percentage of correct classification (after cross-validation) to individuals within
564 each of the 10 study groups compared to that expected by chance. P values are derived from
565 binomial tests using the random % expectation level as the test level.
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566 Figure 1: Time- frequency spectrogram illustrating a meerkat contact call produced during
567 foraging. A: Lowest visible band representing the fundamental frequency (F0). B: Harmonic
568 overtone of the F0.
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570 Figure 2: Bar graph showing the number and type of playbacks specifically for the closest
571 approach to loudspeaker (m) response variable.
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581 Figure 3: Time spent (s) by the focal individual within 5m of the loudspeaker when hearing own,

582 foreign, neighbour and stranger contact calls

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Parameter	Description
df1med	Median frequency of the fundamental frequency, across all time segments (Hz)
q1med	Median frequency of the 1st quartile of distribution of frequency amplitudes, across all time segments (Hz)
q2med	Median frequency of the 2nd quartile of distribution of frequency amplitudes, across all time segments (Hz)
pfmed	Median peak frequency across all time segments (Hz)
pfmaloc noise	Location of the maxiumum peak frequency (between 0 and 1) The percentage of noise in the call
duration n pulses pulse dur interval dur	Duration (ms) The number of pulses per call The duration of the 2nd last pulse (ms) The duration between the 2nd last and the last pulse (ms)

583

Group	Classification %	Random %	N individuals	Binomial test P values
1	65	25	4	P<0.001
2	72.9	11	9	P<0.001
3	61.2	10	10	P<0.001
4	58.9	12.5	8	P<0.001
5	80	16.6	6	P<0.001
6	62.5	12.5	8	P<0.001
7	67.4	11.1	9	P<0.001
8	76.1	20	5	P<0.001
9	72.2	25	4	P<0.001
10	68.8	12.5	8	P<0.001
Mean ± SD	59 ± 7	16 ± 6		

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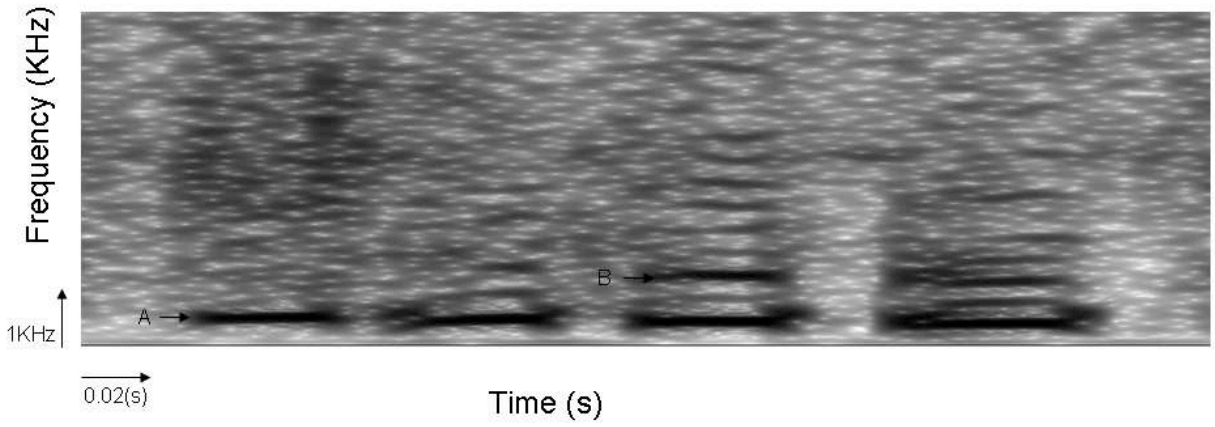

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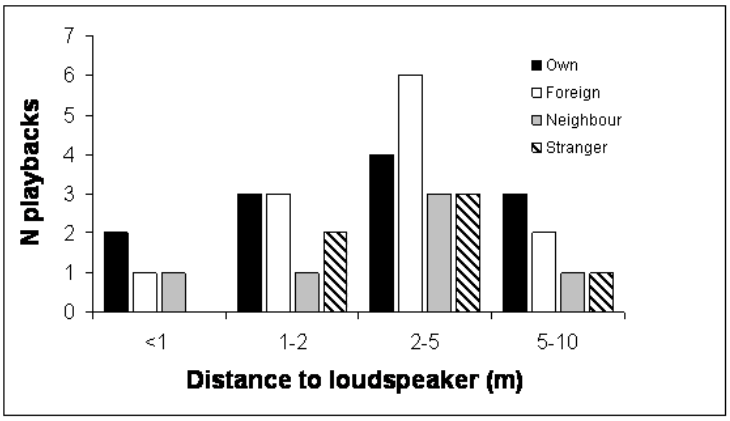
N playbacks
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6
5
4
3
2
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<1
1-2
2-5
5-10
Distance to loudspeaker (m)
Own
Foreign
Neighbour
Stranger

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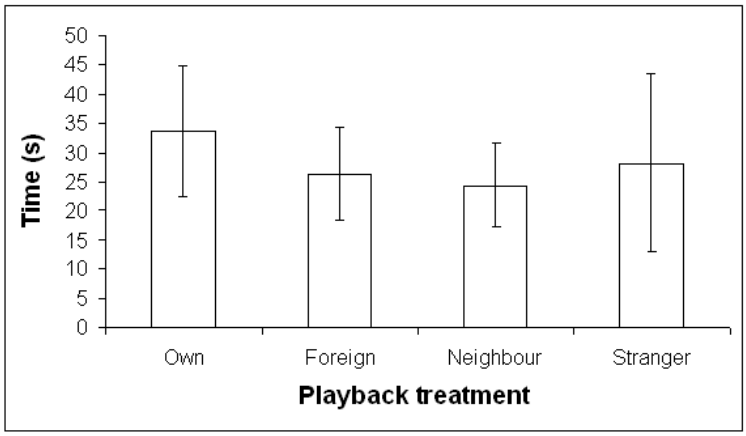
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Time (s)
Own
Foreign
Neighbour
Stranger
Playback treatment

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